

SPATIAL ASSOCIATION BETWEEN A SPIDER WASP AND ITS HOST IN FRAGMENTED DUNE HABITATS

Dries Bonte¹ and **Jean-Pierre Maelfait**^{1,2}: ¹Ghent University, Dep. Biology, Research group Terrestrial Ecology, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium. E-mail: dries.bonte@Ugent.be; ²Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium

ABSTRACT. In patchily distributed habitats, species potentially occur wherever conditions are suitable or show a restricted distribution, influenced by patch quality, geometry and configuration. If patch isolation appears to be the main determinant of the species' distribution then dispersal ability is supposed to be limited. Although only scarce literature is available, dispersal limitation seems to be an important factor in determining the spatial population structure in spiders. In this paper, we document on the spatial population structure of the rare wolf spider *Alopecosa fabrilis*, restricted to fragmented grey dunes along the Flemish coast (Belgium) and ask whether its distribution appears to be affected by aspects of patch configuration. Simultaneously, we investigated whether the local distribution of its main parasitoid, the spider wasp *Arachnospila rufa* (Hymenoptera, Pompilidae) was associated with its host. Our results indicate that *A. fabrilis* shows an aggregative population structure, which is determined by the distance to nearest occupied patch, indicating that spatially correlated habitat quality probably determine its occurrence. Although spider wasps are generally characterized as non-specialists, the almost complete covariation between its spatial occurrence and that of *A. fabrilis*, indicates that spider hunting wasps may, at least temporally and locally, show a restricted host-range. As a result, the presence of a rather generalist parasitoid is a good predictor for the presence of nocturnal and burrowing dune wolf spider.

Keywords: *Alopecosa fabrilis*, Lycosidae, *Arachnospila rufa*, Pompilidae, metapopulations

In fragmented habitats, species live either in patchy populations or in metapopulations (Harrison 1991; Hanski 1999). In patchy populations, individuals move freely among habitat patches, while in metapopulations, most individuals stay in a single patch during their entire life, but dispersing individuals enhance strong colonization-extinction dynamics. This results in a population structure in which some suitable patches remain vacant. Besides the colonization abilities, changes in habitat quality can also attribute to local extinction dynamics, as demonstrated for specialized butterflies (e.g. Thomas et al. 1992; Ravenscroft 1994; Moilanen & Hanski 1998; Bergman 1999) and backswimmers of the genus *Notonecta* (Briers & Warren 2000). Therefore, studying the spatial structure of populations during successive years by considering aspects of patch geometry, quality and configuration enables us to assess actual dispersal limitation and population dynamics in an indirect way. Snapshots of patch-occupancy incidences provide an alternative indirect meth-

odology to study dispersal abilities or populations viability with respect to population size (patch size) resulting from historical habitat fragmentation and population dynamics. As shown for a coastal dune wolf spider, living in fragmented grassland habitats, patch occupancy patterns may depend both on aspects of habitat quality and on different modes of dispersal through the surrounding matrix (Bonte et al. 2003a). For spiders in general, cursorial dispersal and ballooning induce different colonization and extinction patterns, dependent on the species' mobility, its niche breadth and its propensity for aerial dispersal (Bonte et al. 2003a, 2004b). Especially ballooning dispersal appears to be important for occupancy patterns at extended temporal and spatial scales (Bonte et al. 2003a, 2004a), while cursorial dispersal induces short-term colonization events at small spatial and temporal scales (Bonte et al. 2003a). For spiders, direct estimates of realized dispersal are rare and indicate dispersal distances up to few-hundred meters within suitable habitat (Krei-

ter & Wise 2001; Bonte et al. 2003a; Samu et al. 2003) but restricted dispersal up to few meters in unsuitable, often densely vegetated habitat (Bonte et al. 2003a). Indirect estimates of dispersal, estimated by population genetic analyses, are more common (e.g. Boulton et al. 1998; Ramirez & Fandino 1996; Ramirez & Haakonsen 1999; Gurdebeke et al. 2000). In contrast to the latter, studies on occupancy incidences, ideally conducted during several successive years, reveal indirect estimates of dispersal that are independent of historical bottlenecks and selection pressures in spatially structured habitats (Peterson et al. 2001; Bonte et al. 2003a).

In addition to earlier studies on the mobile wolf spider *Pardosa monticola* (Clerck 1757), we here report on the population structure in coastal dune habitats of the specialized fossorial wolf spider *Alopecosa fabrilis* (Clerck 1757) with limited aerial dispersal abilities (Bonte et al. 2003b) and of its main (winged) parasitoid, *Arachnospila rufa* (Haupt 1927) (Hymenoptera, Pompilidae), knowing to host on larger *Alopecosa* wolf spiders (Koomen & Peeters 1993; Peeters et al. 1994). According to theoretical work, host-parasitoid metapopulations dynamics strongly interfere and occupancy patterns should strongly overlap in case of limited host interpatch dispersal abilities and relatively low infection rates and parasitoid survival rates (Hassel et al. 1991; Comins et al. 1992; White et al. 1996; Hanski 1999).

The population structure of parasitoid and host were investigated in the Flemish coastal dunes, where grey dune habitats, being the optimal habitat for both *A. fabrilis* and *A. rufa*, are truly fragmented since the Second World War (see e.g. Bonte et al. 2003a; Provoost & Bonte 2004). This was done in order to test the following hypotheses: (i) *A. fabrilis* has limited dispersal abilities, resulting in an isolation-dependent population structure, (ii) *A. fabrilis*, having low population densities only occupies larger habitat patches and (iii) local and temporal host-parasitoid association result in similar distribution patterns, although Pompilidae have better dispersal abilities and are believed to be rather generalistic in prey choice according to prey species (Finch 1997). Additionally, as *A. fabrilis* is nocturnal while its parasitoid is diurnally active, we asked whether the presence of a day-active parasitoid

could be an indicator for the presence of populations of a nocturnal, fossorial spider.

METHODS

Study Area, Study Species.—Fieldwork was conducted in the Flemish coastal dunes, located between the cities of De Panne (Belgium) and Bray-Dunes, France (51°05'N, 2°32'E) consisting of 52 discrete grey dune patches, varying between 0.05 and 27.6 ha (Fig. 1). Grey dunes, known as "Fixed coastal dunes" are most readily defined using plant communities. Vegetation includes Atlantic moss dominated dunes (mainly *Tortula ruralis*) as well as dune grassland (with a distinct organic soil layer) belonging to the Cladonio-Koelerietalia syntaxon in case of lime rich grey dune, and to the Trifolio-Festucetalia ovinae syntaxon in case of decalcified grey dunes (Provoost et al. 2002). In this study, only grey dunes without substantial soil development were surveyed since they are the habitat of both study species (see further). Ecologically it is merely the dry component of the "stressed dune landscape". The main differentiating processes are related to dune fixation, soil formation and vegetation development (Provoost et al. 2002). At present, rough grass and scrub encroachment result in a severe fragmentation within a matrix of dense dune vegetation (shrubs, dense grassland). In an earlier paper, we identified typical spider species for this habitat (Bonte et al. 2002). One of the most habitat-specific species is *Alopecosa fabrilis*, although its overall Indicator Value was low, hence, indicating a relative low occupancy rate.

Alopecosa fabrilis is used as model organism in this study. It is the largest lycosid species, living in self-made burrows in dry sandy habitats from temperate regions in Europe (males: 10–12 mm; females: 13–16 mm; Roberts 1998). The species has a nocturnal life style in which especially males leave their burrow in search for mating partners during autumn, with a peak activity during September (Roberts 1998; Bonte, unpub. data.). Females are active during autumn, but especially during late winter and early spring. The species occurs in low densities, has a biannual life cycle (Bonte et al. unpub. data) and does not perform ballooning dispersal under laboratory conditions (Bonte et al. 2003b).

During its period of activity, the spider

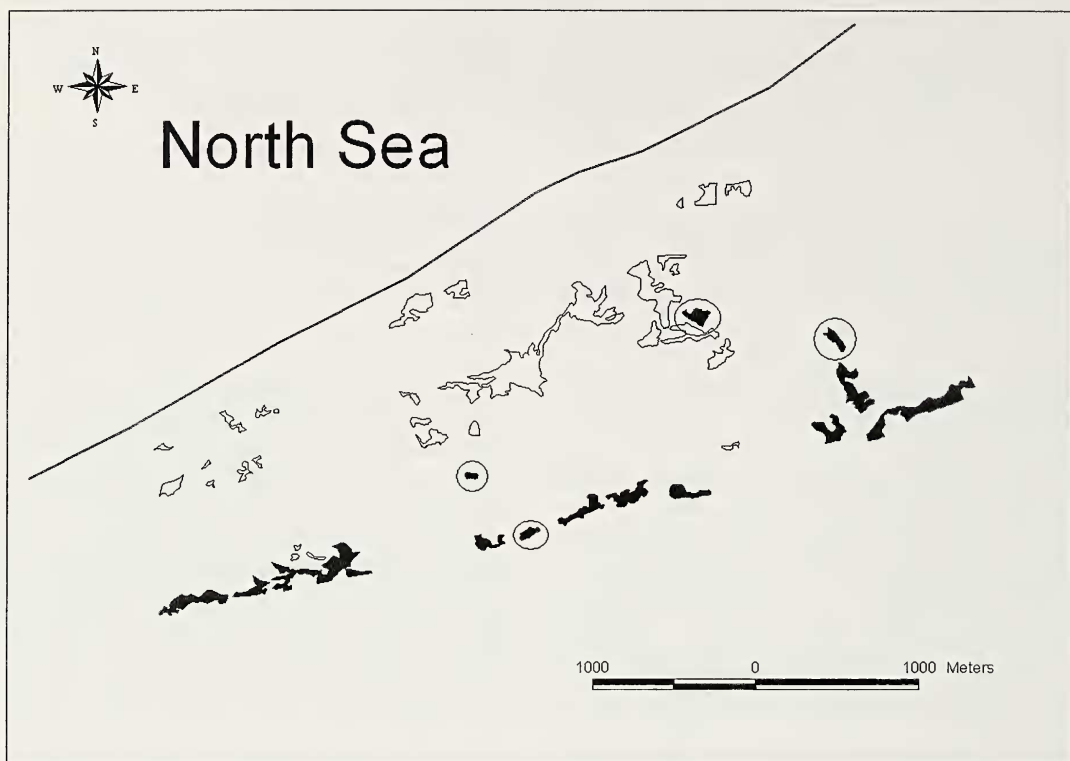


Figure 1.—Map of the surveyed grey dune habitat patches in the coastal dunes of De Panne-Bray Dunes, Belgium. Black: patches occupied by *Alopecosa fabrilis*; white: unoccupied patches. Circles indicate patches not occupied by *Arachnospila rufa*.

hunting wasp (Hymenoptera, Pompilidae) *Arachnospila rufa* has been observed to be the main predator (Koomen & Peeters 1993; Peeters et al. 2004; Bonte, pers. obs.; Nieuwenhuijsen, pers. comm.). *Alopecosa schmidtii* (Hahn 1834) has been recorded as prey in Middle-Europe (Schljachtenok 1996). Female pompilids provide each cell of their nest below the sand surface with only a single paralyzed spider, on which one egg is laid. *Arachnospila rufa* is large (body size up to 18 mm) and common in sandy regions of Belgium and the Netherlands. It reaches adulthood from June–October (Peeters et al. 2004; Nieuwenhuijsen in press). More detailed information about its ecology and life history is unfortunately not available. Voucher specimens of both *Alopecosa fabrilis* and *Arachnospila rufa* are deposited at the Royal Belgian Institute for Natural Sciences.

Field Survey & Statistical Analyses.—Occupancy patterns of *A. fabrilis* were recorded from 25 August–7 October 2003 using pitfall traps (diameter 9 cm, 6% formaldehyde-de-

tergent solution). In each of the 52 grey dune patches, at least five traps were randomly placed, depending on the patch area. Patches were digitized from aerial orthophotographs with a Geographic Information System (Arcview 3.1) and discrimination of vegetation types was based on vegetation-specific red (RED) and near-infrared (NIR) reflectance values (Provoost et al. 2002). Because of its high activity during this season, the use of pitfall traps have been shown to be very useful in catching this typical spider species living within this habitat (Bonte et al. 2004c). The presence of the hunting wasp was recorded in the same pitfall traps, but completed with detailed field surveys during sunny days. Although not all observed specimens were collected to confirm identification, individuals could be identified in the field by their large size and distinct abdominal coloration. From GIS, we measured patch area, the distances to the nearest suitable patch, as a measure of patch isolation and distance to the nearest occupied patch (nearest-neighbor distance) as

measurement of population isolation. For *A. rufa*, we did not use the latter isolation measurement because its presence was only recorded during September, hence ignoring possible different distribution patterns during the previous summer-period.

Patch occupancy patterns for *A. fabrilis* (0: vacant; 1: occupied) were analyzed by logistic models for binomial data and logit-link with backward elimination of the non-significant parameters (SAS 9.2). Patch area, patch isolation and the interaction between both were included as independent variables. For *A. rufa*, the occupancy status of the patch by *A. fabrilis* was used as an additional categorical variable.

RESULTS

Patch occupancy of *Alopecosa fabrilis* was not significantly influenced by patch area ($\chi^2_1 = 2.255$; $P = 0.133$). The distance to the nearest suitable habitat ($\chi^2_1 = 1.168$; $P = 0.280$) and the interaction between both ($\chi^2_1 = 0.208$; $P = 0.648$) did not contribute significantly. If the nearest-neighbor distance was taken into account, a significant negative relationship was found between isolation and patch occupation (estimated slope: -0.035 ± 0.014 ; $\chi^2_1 = 6.322$; $P = 0.012$; Fig. 2). Other parameters remained non-significant. Although the model describes patch occupancy patterns in a significant way, 32.7% of the cases were misclassified. Mainly patches near the inner dune front were occupied (Fig. 1). If only patches at the inner dune front were used for analysis, neither distance to the nearest patch ($\chi^2_1 = 0.028$; $P = 0.865$), distance to the nearest occupied patch ($\chi^2_1 = 1.144$; $P = 0.285$) or area ($\chi^2_1 = 0.476$; $P = 0.490$) explained distribution patterns.

After backward elimination of non-significant parameters, the occupancy of *Arachnospila rufa* was only determined by the presence of *Alopecosa fabrilis* ($\chi^2_1 = 34.41$; $P < 0.0001$). No other lycosid species were recorded during the survey period. Landscape geometry appears to be unimportant during this season since the explanatory power of both patch area and patch isolation are extremely low (all variables and interactions: $\chi^2 < 1.29$; $P > 0.256$). Patches occupied by *A. fabrilis* but not by *A. rufa* ($n = 4$) during this period were significantly smaller than those ($n = 11$) occupied by both species (Mann-Whit-

ney U-test: $Z = 2.74$; $P = 0.006$; Fig. 2). *Arachnospila rufa* was not recorded in patches without *A. fabrilis* populations.

DISCUSSION

Population structure of *Alopecosa fabrilis*.—Our results demonstrate that the distance to the nearest occupied patch contributed significantly to the patch-occupancy model, whereas the overall habitat structure (i.e. geometry and configuration of all available patches) did not. As a result, the population structure seems not to be affected by local potential population sizes (related to local population viability; Hanski 1999) and distant dispersal abilities by ballooning. The latter is in agreement with the absence of aerial dispersal under laboratory conditions (Bonte et al. 2003b). As only the nearest-neighbor distance contributed significantly to the patch-occupancy model, the population structure of *A. fabrilis* seems to be clearly aggregative, indicating low abilities to disperse (and penetrate) cursorially through the hostile matrix or a predominant role of habitat quality. Our data, however, only result from a short term survey. But preliminary data on patch occupancy patterns from 2004 show similar distribution patterns (Bonte et al. unpub. results), indicating the absence of strong turn-over dynamics at extended, though still rather short time spans. The fact that patch area (related to local population size) does not explain occupancy patterns seems to indicate that the spatial population structure is more likely to be determined by random extinction-colonization dynamics within aggregative clusters of closely connected suitable habitat remnants, which appear to be situated near the inner dune front. As the interaction between patch size and patch isolation does not explain occupancy patterns, a rescue effect resulting from source-sink dynamics is unlikely (Dias & Blondel 1996).

The aggregated pattern may result from dispersal limitation after historical population dynamics or from spatially correlated habitat characteristics, related to habitat quality, as experienced by the species. Although both are possible, the second seems to be more probable as especially patches near the inner dune front were occupied. In coastal dunes, characterized by a successive ontogenesis, grey dunes, although structurally similar may show

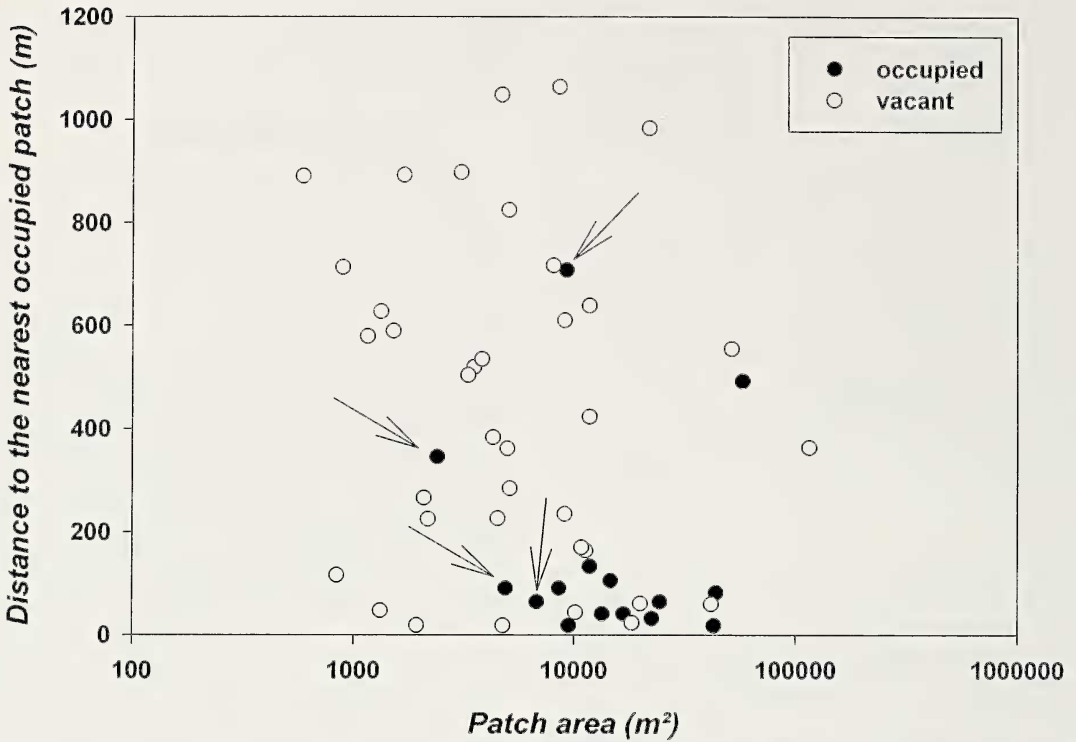


Figure 2.—Relation between patch area, nearest-neighbor distance and occupancy incidence for *A. fabrilis* populations. Arrows indicate patches occupied by *A. fabrilis*, but not by its predator *A. rufa*.

extensive spatial correlation in environmental characteristics related to microclimate, soil properties and aeolic dynamics (sand overblowing). The fact that considerable non-spatial correlated variation in habitat quality affects spatial structural patterns has already been demonstrated by e.g. Briers & Warren (2000) and Bonte et al. (2003a). For a fossorial species like *A. fabrilis*, it is not impossible that e.g., grain size properties, soil water retention, soil formation and the intensity of sand overblowing strongly determine burrowing ability and the sustainability of created burrows. In the same coastal dune landscape, the grassland inhabiting wolf spider *P. monticola* shows a habitat-quality dependent population structure in which both patch area and patch connectivity determined occupancy patterns (Bonte et al. 2003a), although not in an aggregative way. As vegetation structure is alike in all investigated grey dune patches, similarity in habitat quality for *A. fabrilis* is probably more related to pedological (possibly soil stability or differences in grain size near the inner dune front) or microclimatological (less buffered temperatures far from the sea)

conditions and, possibly, the reason for the observed clustered occurrence. Also, the absence of *A. fabrilis* in large patches more close to the sea, in which large populations should be able to persist, provides more likely evidence for a reaction towards spatially correlated environmental properties and optimal habitat quality in older grey dunes, situated near the inner dune front. In this case, dispersal limitation is of inferior importance, as illustrated by the model in which only patches near the inner dune front were included.

Host-parasitoid association.—Spatially explicit host-parasitoid metapopulation models generate spatially correlated abundance and, hence, occupancy patterns in host and parasitoid (Hanski, 1999). *Arachnopsila rufa* and related spider hunting wasps, however, appear to be more generalist parasitoids on (larger) lycosid species (Koomen & Peeters 1993; Endo & Endo 1994; Finch 1997; Peeters et al. 2004). The almost complete match between occupancy incidences of host and parasitoid indicate that, at least in the Flemish coastal dunes and during the survey period, *A. rufa* behaves as a specialized parasitoid on *A.*

fabrilis. This indicates that at least one species of pompilid wasp may behave as a host-specialist during some periods of its adult life. According to White et al. (1996), spatial population patterns in which both host and parasitoid occur in the same patches are only static in case of low host dispersal and low parasitoid survival. Certainly the first assumption seems to be fulfilled in our study. However, *A. rufa* is already adult earlier in the season, and should, as a result, behave more flexibly in prey selection. As predicted by optimal foraging theory, prey size selection should be optimized in relation to the species' load-carrying capacity (Evans 1962; Coelho & Ladage 1999). The latter authors indeed found that large female wasps searched for prey that matched their own body mass and lift capacity. As a result, *A. rufa* should prey on similarly large-bodied lycosid species or show behavioural flexibility according to the available prey spectrum. Taking into account the need for sandy habitats for prey burrowing, *A. rufa* seems to be restricted to dynamic dune habitats in which soil development is poor and bare sand sufficiently available. Female *A. fabrilis* disappear from the population in late winter and early spring and are not available as host during the early beginning of the hunter wasp's adulthood (Bonte, unpub. data). Other large-bodied lycosid species, occurring in these habitats include only *Alopecosa cuneata* (Clerck 1757) and *A. barbipes* (Sundevall 1833) (Bonte et al. 2002), also having a spring activity, and are as a result neither available during summer. Possibly, *A. rufa* uses smaller lycosids as host during early summer (*Arctosa perita* (Latreille 1799) or subadult *A. fabrilis*), potentially resulting in different spatial distribution patterns.

The fact that *A. rufa* was only absent from small patches, inhabited by *A. fabrilis* seems to provide evidence that higher trophic levels require larger habitats (Holt 1996; Holt et al. 1999), but may also be an artifact in our sampling strategy if smaller patches are only accidentally visited by the spider wasp, hence reducing encounter chances in the field. According to Holt (1999), higher trophic ranks need larger areas if dispersal is limited, have closed populations and show a high degree of specialization towards resource species. Certainly the latter seems to hold for the (at least temporal and local) *A. rufa*-*A. fabrilis* asso-

ciation. Assuming that our findings are not due to sampling artifacts, parasitoid absence in small populations indicates low dispersal abilities or at least low dispersal motivation in spider wasp within spatially structured suitable habitat surrounded by hostile matrix vegetation.

Also, since both juvenile and adult *A. fabrilis* stay in their burrow during day, prey selection by *A. rufa* has probably to rely on olfactory and not on visual cues because burrow entrances are not visible, as also observed in spider hunting wasps preying on day-active wolf spiders (e.g., *Pompilus cinereus* (Fabricius 1775); Bonte pers. obs.) and in sphecoid wasps (although only at short distance after visual detection; Anton & Gnatzy 1998).

In fragmented coastal dune habitats, host and parasitoid show, at least temporally and locally, a similar aggregative spatial population structure, indicating the importance of (lack of) dispersal and possibly spatially correlated habitat characteristics in structuring patch occupancy patterns. Additionally, the spider hunting wasp *A. rufa* appears to behave as a specialized parasitoid during the main activity period of its optimal prey with restricted dispersal motivation. During this period, the presence of an assumed generalist parasitoid is a good predictor for the presence of nocturnal and burrowing dune wolf spider in larger habitat patches in the Flemish coastal dunes.

ACKNOWLEDGMENTS

The author would like to thank the Ministry of the Flemish Community (Aminal, Afdeling Natuur) and the Conseil Général du Nord for granting access to their field sites. The senior author is a Postdoctoral Fellow of the Fund for Scientific Research—Flanders (Belgium) (F.W.O.—Vlaanderen). One anonymous referee gave very valuable suggestions with respect to species-area relationships and trophic rank, opening new insights for further research.

LITERATURE CITED

- Anton, S. & W. Gnatzy. 1998. Prey specificity and the importance of close-range chemical cues in prey recognition in the Digger Wasp, *Liris niger*. *Journal of Insect Behavior* 11:671–690.
- Bergman, K.-O. 1999. Habitat utilization by *Lopinoga achine* (Nymphalidae:Satyrinae) larvae and

- ovipositing females: implications for conservation. *Biological Conservation* 88:69–74.
- Bonte, D., L. Baert, & J.-P. Maelfait. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology* 30:331–343.
- Bonte, D., L., Lens, J.-P., Maelfait, M. Hoffmann, & E. Kuijken. 2003a. Patch quality and connectivity influence spatial dynamics in a dune wolf spider. *Oecologia* 135:227–233.
- Bonte, D., N., Vandenbroecke, L. Lens, and J.-P. Maelfait, 2003b. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society London Series B* 270:1601–1607.
- Bonte, D., L., Baert, L., Lens, & J.-P. Maelfait. 2004a. Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. *Ecography* 27:343–349.
- Bonte, D., L. Lens, & J.-P. Maelfait. 2004b. Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider. *Journal of Animal Ecology* 73:643–650.
- Bonte, D., J.-P. Maelfait, & L. Baert. 2004c. Determining spider species richness in fragmented coastal dune habitats by extrapolation and estimation (Araneae). Pp. 189–197. *In* Samu, F & Szinetar, Cs. (eds.). *European Arachnology 2002*.
- Boulton, A.M., M.G. Ramirez, & C.P. Blair. 1998. Genetic structure in a coastal dune spider (*Geolycosa pikei*) on Long Island, New York Barrier Islands. *Biological Journal of the Linnean Society* 64:69–82.
- Briers R.A. & P.H. Warren. 2000. Population turnover and habitat dynamics in *Notonecta* (Hemiptera:Notonectidae) metapopulations. *Oecologia* 123:216–222.
- Coelho, J.R. & L.D. Ladage. 1999. Foraging capacity of the great golden digger wasp *Sphex ichneumoneus*. *Ecological Entomology* 24:480–483.
- Comins, H.N., M.P. Hassel, & R.M. May. 1992. The spatial dynamics of host-parasitoid systems. *Journal of Animal Ecology* 61:735–748.
- Dias, P.C. & J. Blonderl. 1996. Local speciation and maladaptations in the Mediterranean blue tit (*Parus caeruleus*). *Oecologia* 107:79–86.
- Endo, T. & A. Endo. 1994. Prey selection by a spider wasp, *Batozonellus lacerticida* (Hymenoptera: Pompilidae): effects of seasonal variation in prey species, size and density. *Ecological Research* 9:225–235.
- Evans, H.E. 1962. The evolution of prey-carrying mechanisms in wasps. *Evolution* 16:468–483.
- Finch, O.-D. 1997. Spider wasps (Hymenoptera, Pompilidae) as predators of a spider taxocenosis. *Proceedings of the 16th European Colloquium of Arachnology, Siedlce*. Pp. 83–89.
- Guordebeke, S., B. Neiryneck, & J.-P. Maelfait. 2000. Population genetic effects of forest fragmentation in Flanders (Belgium) on *Coelotes terrestris* (Araneae:Agelenidae) as revealed by allozymes and RAPD. *Ekologia (Bratislava)* 19:87–96.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press Inc., New York. 313 pp.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42:73–88.
- Hassel, M.P., H.N. Comings, & R.M. May. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353:255–258.
- Holt, R.D. 1996. Food webs in space: an island biogeographical perspective. Pp 313–323. *In* Polis, G.A. & Martinez, N.D. (eds.): *Food Webs—integration of Patterns and Dynamics*, Chapman & Hall, New York.
- Holt, R.D., J.H., Lawton, G.A. Polis, & N.D. Martinez 1999. Trophic rank and the species-area relationships. *Ecology* 80:1495–1504.
- Koomen, P. & T.M.J. Peeters. 1993. New prey records for spider hunting wasps (Hymenoptera: Pompilidae). *Memoires of the Queensland Museum* 33:571–574.
- Kreiter, N.A. & D.H. Wise. 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia* 127: 417–424.
- Moilanen, A. & I. Hanski. 1998. Metapopulation dynamics: effect of habitat quality and landscape structure. *Ecology* 79:2503–2515.
- Nieuwenhuijsen, H. *In press*. Determinatietabellen voor de Nederlandse spinnendoders (Hymenoptera, Pompilidae). Alkmaar.
- Peeters, T.M.J., C., van Van achterberg, W.R.B, Heitmans, W.F., Klein, V., Lefeber, A.J., van Loon, A.A., Mabelis, H., Nieuwenhuijsen, M., Reemer, J., de Rond, J. Smit, & H.H.W. Velthuis. 2004. *De wespen en mieren van Nederland (Hymenoptera, Aculeata)*. Nederlandse Fauna 6. Nationaal Natuurhistorisch Museum Naturalis, Leiden, K.N.N.V. uitgeverij, Utrecht & European Invertebrate Survey, Nederland, Leiden, 507 pp.
- Peterson, M.A., R.F. Denno, & L. Robinson. 2001. Apparent widespread gene flow in the predominantly flightless planthopper *Tumidagena minuta*. *Ecological Entomology* 26:629–637.
- Provoost, S., C., Ampe, D., Bonte, E. Cosyns, & M. Hoffmann. 2002. Ecology, management and monitoring of dune grasslands in Flanders, Belgium. Pp.11–22. *In* EUROCOAST (ed.): *Littoral 2002, The Changing Coast*. Eurocoast/EUCC, Porto, Portugal.
- Provoost, S. & D. Bonte (eds.). (2004). *Levende duinen. Een overzicht van de biodiversiteit in de*

- Vlaamse kuststreek. Mededelingen van het Instituut voor Natuurbehoud, Brussels, 420 pp.
- Ramirez, M.G. & L.B. Fandino. 1996. Genetic variability and gene flow in *Metepeira ventura* (Araneae, Araneidae). *The Journal of Arachnology* 24:1–8.
- Ramirez, M.G. & K.E. Haakonsen. 1999. Gene flow among habitat patches on a fragmented landscape in the spider *Argiope trifasciata* (Araneae: Araneidae). *Heredity* 83:580–585.
- Ravenscroft, N.O.M. 1994. Environmental influences on mate location in male chequered skipper butterflies, *Carterocephalus palaemon* (Lepidoptera: Hesperidae). *Animal Behaviour* 47:1179–1187.
- Roberts, M.J. 1998. *Spiders of Britain and Northern Europe*. Harper Collins Publishers, London, 383 pp.
- Samu, E., A. Sziranyi, & B. Kiss, 2003. Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. *Animal Behaviour* 66:939–947.
- Schljachtenok, A.S. 1996. Über die Beutespinnen (Aranei) einiger Wegwespen (Hym., Pompilidae). *Entomologische Nachrichten und Berichte* 40(3):169–172.
- Thomas, C.D., J.A. Thomas, & M.S. Warren. 1992. Distribution of occupied and vacant habitats in fragmented landscapes. *Oecologia* 92:563–567.
- White, A., M. Begon, & R.G. Bowers. 1996. Host-pathogen systems in a spatially patchy environment. *Proceedings of the Royal Society London B* 263:325–332.

Manuscript received 16 December 2004, revised 17 June 2005.